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BULLETIN  
OF THE  
TORREY BOTANICAL CLUB

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MARCH, 1910

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The morphology of *Taenioma*

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(WITH PLATES 9 AND 10)

The work here described was done in the Botanical Laboratory of Barnard College, Columbia University, under the direction of Professor H. M. Richards, for whose kindly interest and assistance, as well as that of Dr. T. E. Hazen, I wish to express my deep appreciation. I am greatly indebted also to Dr. M. A. Howe of the New York Botanical Garden, through whose kindness the material has been available for this work. The material used was collected by Dr. Howe on two of his southern trips and was preserved with the aid of formaldehyde as well as by drying. The fertile plants, possessing all the kinds of reproductive organs, were obtained in Porto Rico in 1903; sterile (rarely tetrasporic) plants were collected in the Bahamas (West Caicos) in 1907.

It is not the purpose here to determine the species to which these two plants belong. There are minor differences between them. The plant from Porto Rico (antheridial, cystocarpic, and tetrasporic) appears larger, is dark violet in color, less secundly branched, and the short flattened shoots are longer, sometimes 15-30 segments in length, are more closely and more conspicuously fasciculate or even fastigiate, and are prolonged into three hairs; while the plant from the Bahamas (sterile or rarely tetrasporic) is smaller, reddish purple in color, the branches are apparently more secund and the short flattened shoot, 9-15 segments in length, are prolonged into two hairs. In spite of these differences there seems little reason to doubt that both of these plants belong to the spe-

[The BULLETIN for February, 1910 (37: 51-96), was issued 5 Mr 1910.]

cies *Taenioma macrourum* (Schousb.) Thuret.\* According to Falkenberg ('01) the *Taenioma macrourum* which he found near Naples had short shoots ending in two hairs and but 15–20 segments long, which is somewhat longer than the specimen from the Bahamas; otherwise the two agree. The Bahamian plant also agrees with the *Taenioma macrourum*, as described originally by Thuret ('76) from plants collected by Schousboe in Tangier, as far as can be determined by the figures given and by the somewhat condensed description. Agardh ('63) alone notes that the flattened shoots are often prolonged into three hairs, but he is writing of *Taenioma per-*

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\* [EDITORIAL NOTE.—From a study of Thuret's description and figures of his *Taenioma macrourum*, based on Schousboe's plant from Tangier, Morocco (*Polysiphonia macroura* Schousb. in herb.), Miss Thompson seems to be justified in identifying at least the Bahamian plant with this species. But the question still remains as to the identity of this *T. macrourum* with the previously described *Taenioma perpusillum* of J. Agardh, based on material collected on the Pacific coast of Mexico. Thuret had not seen Agardh's specimen, but in proposing Schousboe's as a different species, he was influenced by the widely separated stations of the two plants, by some apparent differences in size and color, judging from Agardh's description, and by Agardh's alleged silence as to the apical division of the stichidium and the elongation of its divisions into two hyaline hairs. Agardh, however, does state that the stichidia are often excurrent at the apex "in fila minuta 3." I have had the opportunity of comparing Agardh's original specimen of *Taenioma perpusillum* (*Folysiphonia perpusilla* J. Ag. Öfv. Kongl. Vet.-Akad. Förh. 4: 16. 1847), in the Agardh herbarium at Lund, with my specimen from Porto Rico (Aguadilla, June 15, 1902, no. 2433) and find them essentially the same except that the terminal hairs are much longer and more luxuriant in the Porto Rican plant. In the original *T. perpusillum* the stichidia often terminate in three short hairs, as described by Agardh. My Bahamian specimens (West Caicos, December 20, 1907, no. 5708) differ in several respects from the Porto Rican, as indicated above by Miss Thompson. However, they are mostly sterile and they were found growing in an inland pond or lake, having, evidently, a subterranean communication with the sea—a place where several marine algae of recognizable species were more or less abnormal and peculiar. The color of these specimens when dry is reddish purple instead of the sordid green attributed to *T. macrourum* by Thuret and the terminal hairs (always, apparently, in twos) are commonly shorter than in the figures published by Bornet & Thuret and by Falkenberg, though often longer than any figured by Miss Thompson. In the Porto Rican specimens, the terminal hairs, which are nearly always in threes, though rarely in twos, are fully as long and as well developed as those figured by Bornet & Thuret and by Falkenberg for *T. macrourum*, though one, perhaps, might not infer this to be the fact from the figures drawn by Miss Thompson. The Porto Rican plants, by the way, were growing where they were well exposed to the surge of the open sea. From the evidence thus far available I am inclined to agree with Bornet (Mem. Soc. Nat. Sci. Cherbourg 28: 297. 1892), with Heydrich (Hedwigia 33: 295. 1894), and with De-Toni (Sylloge Algarum 4: 732. 1900) in considering *Taenioma macrourum* (Schousb.) Thuret a synonym of *Taenioma perpusillum* J. Ag.—M. A. H.]

*pusillum* J. Ag. and not of *T. macrourum* (Schousb.) Thuret. However, although it would seem probable that both of my specimens should be classed with *T. macrourum*, a discussion of the classification would not be profitable here, since this work concerns itself not with a determination of species, but with a description of the exact method of growth and cell division, and the appearance and formation of the reproductive organs.

The species of *Taenioma* studied is a small marine alga, forming dense tufts on other algae, or on sticks of wood near the low-water line. It is purplish red or dark violet in color, and minute in size as to the individual plants, though forming, in mass, patches easily distinguishable. The main axis is monopodial, siphonous, branched, creeping, segmented, and not corticated, and is attached to the substratum by numerous rhizoids (FIG. 1). Branches arising from the main stem are in turn much branched, frequently forming long secondary axes, which are prostrate and produce rhizoids. The shorter secondary axes are erect, arising alternately from either side of the stem, those on the lower side twisting in the process of erection, so that superficially they appear secund. Both these and the main shoot bear short flattened shoots, arising alternately, and prolonged at the apex into two or three long monosiphonous hairs. Growth takes place by means of a single apical cell which is recorded by Agardh ('63) as dividing dichotomously. Since the cell does not divide by a longitudinal split, as will be shown later, and since the main axis is monopodial, this cannot be considered true dichotomy, although the branching may be called subdichotomous.

The rhizoids are numerous, arising irregularly, each being a direct prolongation of any pericentral cell on the under side of the thallus. They are unicellular, often of considerable length, with ends rounded or spread out into disks or forked projections (FIG. 2).

The main stem or primary monopodial axis of the plant is composed of four pericentral siphons in protoplasmic connection with each other and with the central siphon. This latter forms a distinct core through the stem, the cells being elongated and closely joined, with deep pit connections. A stem segment is cylindrical, composed of four of these pericentral cells with the corresponding axial cell. No evidence of cortication has been

observed at the joints, even in the oldest portions. The method of growth is by a single dome-shaped apical cell, which cuts off disk-shaped cells at its base, each of which will correspond to a single segment in the fully formed stem. When the formation of a branch is to take place, the apical cell divides by an oblique wall into two unequal parts. The smaller of the two is the cell which will continue the main axis; the larger increases laterally and divides by an oblique wall at right angles to the first. This second dome-shaped apical cell forms the apical cell of a secondary axis (FIG. 4). Hence it is evident that this branching is not true dichotomy, since the two newly formed apical cells are not the product of the single division of an apical cell. The cell of the shoot tip is the true apical cell, for the branch apical cell is formed secondarily by the further growth and division in a cell underlying the tip cell. The apical cell of the tip next cuts off 3-6 disk-shaped segments below, in which soon appear two longitudinal divisions, separating these segments into three cells in a row in one plane.\* Somewhat later and usually just behind the first branch formed from the tip, two other longitudinal divisions, parallel to each other and perpendicular to the first division, occur in the middle cell, forming the other two pericentral cells. Consequently in the fully formed stem the branches are separated by three to six segments, whose structure superficially resembles that of a simple *Polysiphonia* (FIG. 3).

The secondary axes develop in the same way as the main shoot, from the apical cell mentioned above. They may be short and erect with but 2-6 branches (FIG. 1), or they may be long and recumbent, giving rise to similar tertiary axes. On them as lateral outgrowths appear the flat short branches, and also the reproductive organs, the stichidia with tetraspores, the antheridia, and the cystocarps.

The flat shoots (FIG. 11) arise in the following manner: An apical cell of the axis divides into a growing tip cell and a branch cell as before (FIG. 4). This branch apical cell cuts off below disk-shaped segments until a filament of 9-30 cells is formed (FIG. 7). It then divides as did the apical cell into two, from

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\* Longitudinal will be used throughout as indicating a division parallel to the axis; transverse as across the plant.

which come the long narrow monosiphonous hairs (1-many cells in length) at the apex (FIGS. 6, 7, 8). In the case of the plant having three hairs, the formation of the third hair presents no variation. After the second apical cell has been separated off, the larger lower cell again increases laterally and a third cell is formed by division. After the hairs begin their formation no further transverse split takes place in the branch cells already formed, thus fixing definitely at this point the number of segments in a mature branch. The first divisions of the branch cells are similar to those of the stem. Two longitudinal divisions split the filament into a plate of cells in three rows (FIG. 10). But now a characteristic change takes place in the two outer rows. In these cells an oblique wall, first occurring in the upper half, splits off a triangular cell one third the size of the original, then a second of like shape and size in the lower half, forming three cells: an inner pericentral cell of the same height but one half the width, and two outer marginal cells, one lying above the other, one half as long and one half as wide as the original cell (FIG. 9). Simultaneously with these divisions two longitudinal ones in the central row of cells divide it into a midrib, three cells in thickness. These divisions all begin at the base of the branch and proceed to the apex. A flat-branch segment in distinction from an axis segment now consists of nine cells; three in the midrib, a pericentral cell on each side of the midrib, and beyond each of these two small marginal cells. These segments are of a similar structure throughout the branch with the exception of 2-4 at the base, which do not form the small marginal cells, but have four pericentral siphons like those of the main axis.

Up to the present time, so far as my knowledge goes, the tetraspores have been the only known organs of reproduction of *Taenioma*. These have been mentioned both by Bornet and Thuret, and by Agardh. Bornet and Thuret ('76) merely figure and describe very briefly the gross appearance and position of the stichidia with no account of the tetrasporic formation. Agardh ('63) gives a fuller account, but yet does not satisfactorily present in detail all cell divisions taking place in the stichidia. This account will supplement both the above, as well as the later description and figures given by Falkenberg. In the material examined,

both the Porto Rican plant with the three-haired branches, and the Bahamian one with the two-haired branches produced tetrasporic stichidia. Agardh ('63) speaks of the stichidia as "often excurrent at the top into three minute hairs, of which the middle one continues the middle part of the segment [*i. e.*, the midrib] the marginal ones the marginal cells" [translation]. This corresponds exactly to my Porto Rican material. There the tetrasporangia are formed in stichidia on the flat shoots of the secondary axes in considerable number (FIG. 12). These stichidia are flat branches which remain practically unmodified except that, with the formation of the large tetraspores, they become somewhat broader. The tetrasporangia are formed in two long rows from the two pericentral cells which lie one on each side of the midrib. A transverse division first separates these cells into an upper and a lower half (FIG. 13). The upper half becomes the mother-cell of the tetraspores. The lower half divides by two longitudinal divisions parallel to the flat surface of the branch into a layer of three cells in thickness. These become crowded and elongated in a radial direction by the growth of the tetraspore mother-cells. The upper half of the pericentral cell enlarges greatly to form the tetraspore mother-cell, which still remains in protoplasmic communication with the lower layer of supporting cells. To form the tetraspores, the contents of the mother-cell divide first into two by a longitudinal wall parallel to the flat surface of the stichidium (FIG. 14). A transverse division forms two tetraspores from one half, and another division, at right angles to the planes of the first two divisions, correspondingly forms the two in the second half. These are therefore one form of "cruciate" tetraspores. They are held within the mother-cell wall, which breaks when mature, allowing the tetraspores to escape. These lateral pericentral cells are the only ones to be modified, the midrib and the marginal cells being unchanged. The entire branch or only a portion of it may be transformed into a stichidium.

Little has been known heretofore concerning the antheridia. Falkenberg ('01) figures a shoot bearing two large conical protuberances, seemingly filled with, or composed of, small cells, but he rightly concludes that these are malformations and not antheridia. De-Toni ('00) mentions antheridia as spots between the

middle vein and the margins of the branches, a description which does not wholly correspond to the antheridia as seen in the material at hand. In this, antheridia are formed, as are the tetrasporangia, in ordinary flattened branches, clustered near the growing tips of the secondary axes (FIG. 15). The entire branch (with the exceptions noted below) is usually transformed into antheridial cells, although these may be found only in the middle portion, while the cells at base and apex of the branch remain unchanged. In the formation of the antheridia the first divisions occur in the row of marginal cells. A longitudinal split cuts each into two (FIG. 17). After the first division of the marginal cells into two, the outer row of these never divides again, so that, in the mature antheridium, there is always to be seen a row of marginal cells one half the size of the original ones (FIG. 18). The inner row divides irregularly into many small cells. The lateral pericentral cells now become modified, being cut by both longitudinal and transverse divisions into numerous small cubical cells (FIG. 16). Before these are entirely completed, a longitudinal split parallel to the flat surface of the shoot takes place. This causes the shoot to become a flattened plate of small angular cells, two layers of cells in thickness, with two exceptions: (1) the midrib, which remains entirely unchanged, and (2) the marginal cells. Next, the true antheridial cells are separated from these mother-cells in the two layers on the side toward the surface of the flat shoot (FIG. 19). These very small, ovoid bodies, containing the spermatia, are all in protoplasmic connection and are formed 2-4 to a mother-cell, 4 being probably the normal number. At regular intervals in the antheridial branch there can be noticed a faint line of separation from the midrib to the margin, denoting the original separation of cells into segments (FIG. 15).

Although the tetraspores have been known since the plant was first described, and the presence of antheridia has more recently been alluded to, the cystocarp has been absolutely unknown. De-Toni ('00) says specifically "*Cystocarpia ignota*" and other literature on the subject does not mention them at all. It has been my good fortune to find in the material collected at Porto Rico a number of cystocarpic specimens. Unfortunately the material has not afforded sufficient stages to trace the growth of the cystocarp from its beginning, nor has there been a sufficient number of



mature cystocarps to make sectioning by microtome possible. The young material was not satisfactory. No procarps were distinguishable as such, although in several instances there appeared to be distortions of normal cells, forming slight protuberances, looking like small malformed branches in some cases. Here indications were found of a row of three small cells which led me to consider the possibility of these being unfertilized and disorganized procarps. In no case was a trichogyne found. The young stages of the cystocarp, when crushed, lost all cell connections, so that no details of their interior structure could be seen. The mature cystocarp from its position is a modified branch, and is situated directly on an axis, not on a flattened branch (FIG. 20). It is a prominent flask-shaped, sessile body, resembling that of *Dasya*, with a large rounded base containing the carpospores, and a long narrow neck which opens at the tip by a distinct carpostome. (The cystocarp pictured is not fully mature, hence the neck is shorter than normal.) The outer covering of cells appears to be continuous with the pericentral cells, and thus probably developed from them. The wall cells are irregularly angular and one layer in thickness. By crushing the material and noting the position of parts, the cystocarp appears to correspond in many details with those of the Rhodomelaceae, especially with those of *Dasya* and *Chondria*, as described by Phillips ('96). The paranematal filaments which he mentions in all these forms are here very apparent; they consist of about 12 chains of cells springing from the base of the cystocarp; but their origin could not be distinguished. These filaments extend to the carpostome. They are narrow and distinct, and do not form in any sense an inner lining to the cystocarp. Also, on crushing, the following structures appeared to constitute the inner apparatus of one cystocarp, which structures were later confirmed by those from a second (FIG. 21). In both cases a comparatively large central cell bore at its apex, by deep pit connections, four large rounded cells. From these proceeded long branching filaments, the sporogenous filaments, on whose tips were borne the large ellipsoidal carpospores. At the base of this central cell was attached a single cell, in the first case examined, and three cells in the second case. Since the central cell was larger in the first, it might be suggested that the cystocarp was older and that a process of absorption of the surrounding cells by the central cell (an auxiliary cell?) was

taking place during the formation of the carpospores. In the second case, not pictured here, one of the lower lateral cells is producing a mass of branching filaments. In two other cystocarps, before crushing, a cluster of filaments was observed at the base of the true spore clusters. This cluster was formed of small elongated cells, densely branching, and apparently without carpospores. Although their connection with the main cells could not be discovered, the question suggested itself: might these not be the two branches of sterile cells found by Phillips ('95, '96) in all the Rhodomelaceae? From this necessarily incomplete account, which merely suggests the identity of the structures observed, it can be seen that much more investigation remains to be done on the cystocarp.

According to the classification of Schmitz & Hauptfleisch ('97), *Taenioma* is placed in the family Delesseriaceae. This position is determined from the similarity of the thallus to those of some members of that family, such as the well-known *Caloglossa*, and also from the formation of the tetraspores in two rows along a midrib. This would seem logical when the tetrasporic reproduction was the only method known. However, with the discovery of the cystocarps, and their strong resemblance to those of *Dasya* and *Chondria*, as described by Phillips ('96), it would seem as if *Taenioma* had been wrongly placed, and that it belongs in the family Rhodomelaceae. The structure of the thallus and the method of branching, resemble that of the simpler members of the Rhodomelaceae and the formation and position of the tetraspores are not such as to exclude it from this latter family. Indeed, from Hauck's ('85) description of the placentation of the cystocarp it must belong here. According to his descriptions the distinguishing mark of the Delesseriaceae is the broad basal placental cell of the cystocarp, from which the sporogenous filaments come in clusters. In distinction to this the placentation in the cystocarps of the Rhodomelaceae is an upright central cell bearing the branching sporogenous filaments at its apex. On comparison with FIG. 21, the latter method of placentation is clearly recognized to obtain in *Taenioma*, which undoubtedly would cause this alga to be placed in the family Rhodomelaceae.

## LITERATURE CITED

- Agardh, J. G.** Species, genera et ordines algarum 2: 1256, 1257. 1863.
- De-Toni, J. B.** Sylloge algarum 4: 731-733. 1900.
- Falkenberg, P.** Die Rhodomelaceen des Golfes von Neapel. Fauna und Fl. Golf. Neap. Monog. 25: 709-711. *pl.* 15. *f.* 21-29. 1901.
- Hauck, F.** Die Meeresalgen Deutschlands und Oesterreichs. Rabenhorst, Krypt.-Fl. Deutsch. Oesterr. und Schweiz 2: 169. 1885.
- Oltmanns, F.** Morphologie und Biologie der Algen 1: 593, 595, 659-662. 1904.
- Phillips, R. W.** On the development of the cystocarp in Rhodomelaceae. Ann. Bot. 9: 289-305. *pl.* 10. 1895; 10: 185-204. *pl.* 12, 13. 1896.
- Schmitz, F., & Hauptfleisch, P.** Delesseriaceae. Engler & Prantl, Nat. Pflanzenfam. 1<sup>2</sup>: 409, 415. 1897.
- Thuret, G.,** in Bornet & Thuret, Notes algologiques 69. *pl.* 25. 1876.

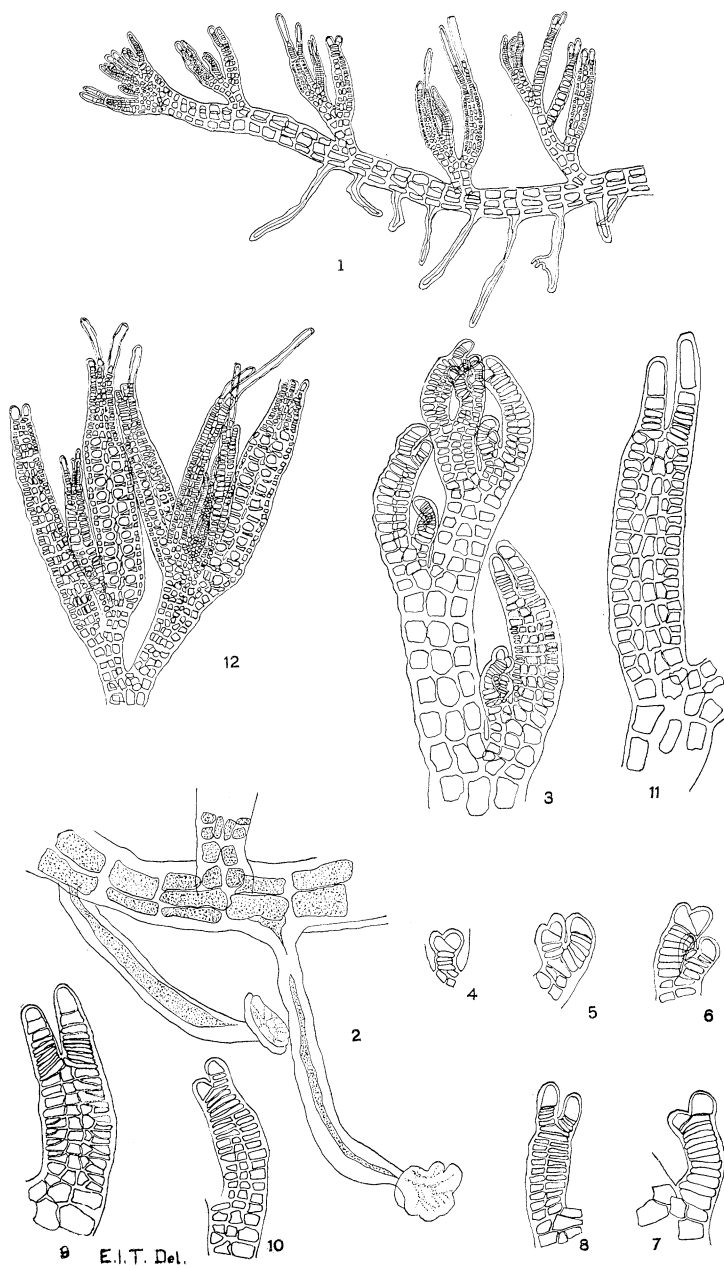
## Explanation of plates 9 and 10

Slides were prepared by staining with eosin and fixing with acetic acid, and by further treatment with potash and lactic acid.

Drawings were made with an Abbé camera lucida, and are reduced one half.

Figures 1-11 were drawn from the Bahamian material; figures 12-21, from the Porto Rican.

1. Portion of the prostrate main axis ( $\times 45$ ).
2. Segment of the axis with rhizoids ( $\times 107$ ).
3. Growing apex, showing alternation of branches ( $\times 107$ ).
- 4-11. Development of flat shoot ( $\times 278$ ).
4. Division of apical cell.
5. Main axis with young branch.
6. Division of apical cell to form hairs.
7. Branch showing filament of cells.
- 8, 10. First longitudinal divisions of shoot.
9. Divisions forming marginal cells.
11. Fully formed shoot.
12. Branch bearing stichidia ( $\times 45$ ).
13. Portion of stichidium, showing division of pericentral cells to form tetrasporangium ( $\times 278$ ).
14. Mature stichidium with fully formed tetraspores ( $\times 278$ ).
15. Branch with antheridia ( $\times 45$ ).
- 16-19. Development of antheridia.
16. Divisions in pericentral cells ( $\times 278$ ).
17. First division of marginal cells ( $\times 107$ ).
18. Portion of discharged antheridium ( $\times 360$ ).
19. Antheridial cells with mother cells ( $\times 360$ ).
20. Branch with cystocarp ( $\times 45$ ).
21. Interior cells of cystocarp ( $\times 278$ ).



THOMPSON: MORPHOLOGY OF TAENIOMA

